1993. Pages 34-45 *in* Luring Lampreys: Assessing the Feasibility of Using Odorants to Control Sea Lamprey in the Great Lakes. Workshop sponsored by Great Lakes Fishery Commission, (October 29-31, 1993, Marine-on-Croix, Minnesota)

III.2. Sulfur-containing Semiochemicals Attract Predators and Repel Prey (Russell Mason).

Background--Dr. Russ Mason is a psychologist who received his M.A. and Ph.D. degrees from Clark University. Following post-doctoral training at Brown University and the Monell Chemical Senses Center, Russ became an Assistant Member on the regular Monell staff. In 1986, he accepted a position with the Denver Wildlife Research Center. At present, Dr. Mason is a project leader for the Wildlife Research Center, and an Associate Member at Monell. He also has faculty appointments at the University of Pennsylvania (Biology) and Rutgers University (Animal Sciences).

Submitted manuscript--Regardless of vertebrate class, carnivores and omnivores are attracted by sulfurous odors and herbivores are repelled by them. This is especially true in feeding contexts. The present manuscript seeks to provide a plausible explanation for this dichotomy. As a background for the explanation, several illustrative examples are provided below.

When faced with a choice among feeding sites, Norway rats prefer locations that conspecifics are exploiting (Galef and Clark 1971, Galef and Heiber 1976). When faced with a choice among several novel foods, naive rats choose the types of novel foods that have previously been ingested by conspecifics with whom they have interacted (e.g., Strupp and Levitsky 1984). This socially mediated transfer of food preference is semiochemically mediated (Galef and Wigmore 1983, Galef and Stein 1985).

Important chemical information could be simply the smell of food. However, transmission appears to involve both the smell of the ingested diet and an endogenous (demonstrator-derived) cue (Galef et al. 1985, Galef and Stein 1985). Behavioral and gas chromatographic/mass spectroscopic experiments suggest that 1-10 ppm carbon disulfide and/or carbonyl sulfide are critical components of the endogenous signal (Bean et al. 1988, Galef et al. 1988). Carbon disulfide is as attractive to wild rats as it is to rats in the laboratory (Mason et al. 1988), and in standardized tests, carbon disulfide improves the acceptance of EPA challenge baits by wild-trapped Norway rats (Figure 1).

Carbon disulfide and other sulfurous compounds are also attractive to dogs and cats. Diallyl disulfide (garlic) is a popular flavor additive to both dog and cat foods (D. Passe, personal communication), and both diallyl disulfide and propane thiosulfinate (onion) enhance consumption by these carnivores (Mason, unpubl. obs.). Since successful coyote (Canis latrans) lure formulations contain sulfurous materials (G. Preti, unpubl. obs.), it seems likely that sulfurous compounds are attractive to these canids as well.

Anecdotal and experimental evidence support the view that sulfur-containing compounds are repellent to herbivores. Grazing ungulates such as mule deer (Odocoileus hemionus) and elk (Cervus canadensis), herbivorous rodents like mountain beaver (Aplodontia rufa), and lagomorphs like cottontailed rabbits (Sylvilagus floridanus) are repelled by hydrogen sulfide (Campbell, and Evans, 1988, Conover 1987, Conover and Kania 1987, DeVoe and Schaap 1987), an odorant that attracts coyotes (Bullard pers. commun.).

The omnivore-carnivore/herbivore dichotomy spans vertebrate classes. Among birds, there is evidence that carnivores such as turkey vultures (Cathartes aura) find food on the basis of sulfur-containing volatiles (Stager 1967, Houston 1986). Conversely, herbivorous species such as Canada geese (Branta canadensis) avoid plants like wild onion (Mason, unpubl. obs.), perhaps because these plants contain S-propyl propane thiosulfinate. Among fish, the use of sulfur-containing baits for catfish (Ictalurus nebulosus) is well-known, and sulfur-containing amino acids like cysteine and methionine are potent olfactory and taste stimuli (Caprio 1975, 1977).

One plausible explanation for the attractiveness of sulfurous odorants to carnivores and omnivores and the repellency of these same materials to herbivores is that sulfur is released during the bacterial degradation of proteins. Thus, the presence of sulfur could indicate that an animal has recently consumed meat--a fact that should attract carnivores and omnivores, but repel herbivores. It also follows that other excreta (urine, feces) should be repellent to herbivores. There is evidence consistent with this possibility. For example, the urine of a variety of arbitrarily selected predators is repellent to mountain beavers (Aplodontia rufa) when the odors are presented in the immediate vicinity of a food source (Epple et al. 1993; Figure 2).

Studies on a number of other mammals, including lagomorphs, rodents, and ungulates also document the effectiveness of predator-derived chemical cues as herbivore repellents. Feces, urine, and glandular secretions affect spacing, exploitation of food resources and damage to plants by some old world and new world Lagomorpha (Sullivan et al. 1985a, Sullivan and Crump 1984, 1986a, Robinson 1990), several species of Microtus (Stoddart 1976, 1980, 1982, Dickman and Doncaster 1984, Gorman, 1984, Sullivan and Crump 1986b, Sullivan et al. 1988a,b, 1990a, Robinson 1990), woodchucks (Marmota monax, Swihart 1991), and Norway rats (Rattus norvegicus, Vernet-Maury 1980, Vernet-Maury et al. 1984). Not surprisingly, predator odors are being evaluated as practical repellents under field conditions. Extensive laboratory and field studies by Sullivan and co-workers, testing a number of synthetic components of predator scent, resulted in a potential new rodent repellent comprised from 2 constituents of mustelid anal gland secretion (Sullivan and Crump 1986a, 1986b, Sullivan et al. 1988a, 1988b, 1990a, 1990b, Merkens et al. 1991). Both of these secretions are sulfur-containing.

Fecal material and urine from a variety of carnivores reduce feeding in ungulates, including roe deer (Capreolus capreolus), red deer (Cervus elaphus), black-tailed deer (Odocoileus hemionus columbianus), white-tailed deer (Odocoileus virginianus) and domestic sheep and cattle (Van Haaften 1963, Muller-Schwarze 1972, Melchiors and Leslie 1985, Sullivan et al. 1985b, Abbott et al. 1990, Pfister et al. 1990, Swihart et al. 1991, Weldon 1990). Very slow habituation to predator-derived chemical cues was evident in several of these studies (Sullivan and Crump 1984, Sullivan et al. 1988a, Swihart 1991).

Although the repellency of predator odors is influenced by habitat characteristics (Merkens et al. 1991), and other ecological factors (Swihart et al. 1991), there is evidence that avoidance is innate and mediated by a few key chemical cues. For example, many herbivores are repelled by chemical cues from carnivores that do not prey on them (Abbott et al. 1990, Dickman and Doncaster 1984, Gorman 1984, Muller-Schwarze 1972, Stoddart 1976, 1980, 1982, van Haaften 1963). Mountain beavers even avoid feeding from bowls scented with urine from domestic dogs. Similarly, other herbivores are repelled by chemical cues from carnivores that do not normally prey upon them.

Although data are sparse, there is evidence that fish respond to predator odors as mammalian prey do. Fathead minnows (Pimephales promelas) are repelled by the odor of northern pike (Esox lucius) (Chivers and Smith 1993). Likewise, brook trout (Salvelinus fontinalis) are repelled by the odor of Atlantic salmon (Salmo salar) (Keefe 1992). Repellency is influenced by the nature of the salmon's diet, and is significantly enhanced when salmon are eating fish (rather than invertebrates).

Semiochemicals in feeding situations are usually (if not always) sulfur-containing. In part, the repellent or attractant effectiveness of these cues is related to volatility, i.e., more volatile stimuli are more powerful cues. But volatility alone does not explain why sulfur-containing odors should be more important than other equally volatile stimuli. One explanation may be that sulfur-containing odorants are important because they reflect protein digestion. Protein digestion is an indicator of diet type. Hence, the attractiveness of sulfur compounds to carnivores and omnivores, and the repellency of these substances to herbivores. This explanation is similar to a hypothesis proposed by Albone (1984) for air-breathing vertebrates, and incorporates aspects of Bryant and Atema's (1987) explanation of the relationship between diet type and social behavior in catfish. Regardless, sulfur-containing odorants may be especially useful as vertebrate pest control agents because these odors are both attractant and repellent, depending upon the animal under consideration.

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Table 1. Results of choice tests during a diet manipulation experiment with juvenile brook trout from Angeline Brook (AB) and Beaver River (BVR).

Population	Experimental Group	Stimulus Choice	Mean Time Spent	Standard Error
AB	1	CW vs. ATS-M	124.8 217.8	21.3 39.2
	2	CW vs. ATS-G	182.6 124.8	14.4 27.8
	Control	CW vs. CW	129.5 113.9	21.8 22.1
BVR	1	CW vs. ATS-M	181.7 180.2	16.3 14.5
	2	CW vs. ATS-G	252.0 148.8	18.9 34.1
	Control	CW vs. CW	144.8 157.2	16.7 28.6

Abbreviations: CW, control water; ATS-M, Atlantic salmon fed mealworms; ATS-G, Atlantic salmon fed goldfish. From: Keefe, M. L. (1993). Chemically mediated avoidance behavior in wild brook trout, Salvelinus fontinalis: the response to familiar and unfamiliar predaceous fishes and the influence of fish diet. Can. J. Zool. 70, 288-292.

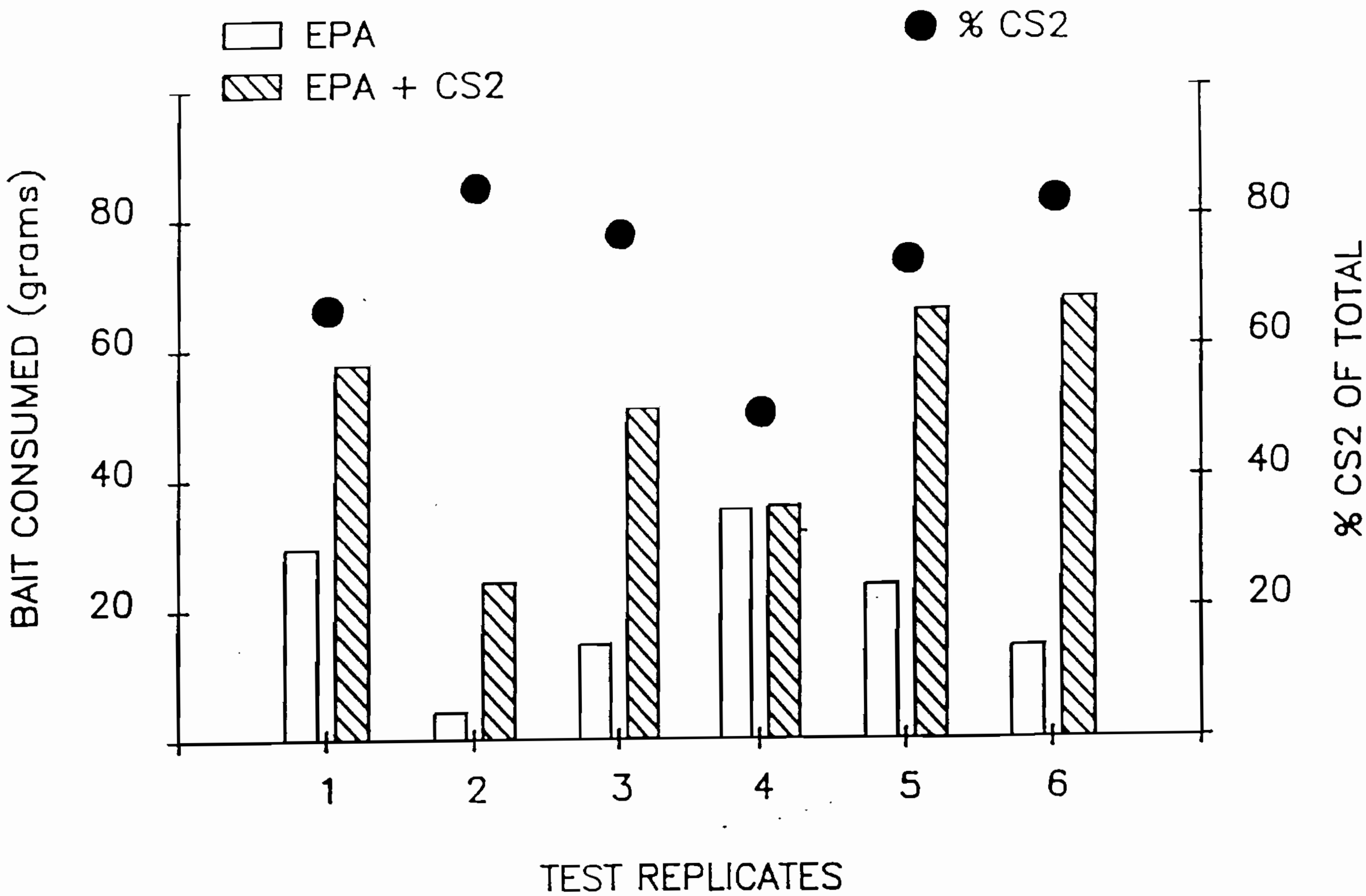
Figure Captions

Figure 1. Consumption of carbon disulfide adulterated EPA challenge bait and control bait by wild-trapped rats. (From: Mason, J. R., N. J. Bean, and B. G. Galef. 1988. Attractiveness of carbon disulfide to wild Norway rats. Proc. Vertebr. Pest Conf. 13: 95-97).

Figure 2. Mean consumption of apple paired with control odors, predator odors, or mink anal gland secretion by mountain beaver. Abbreviations: GPU = guinea pig urine, BA = butyric acid, A = dog, B = mink, C = bobcat, D = coyote. (From: Epple, G., J. R. Mason, D. L. Nolte, and D. L. Campbell. 1993. Effects of predator odors on feeding in the mountain beaver (*Aplodontia rufa*). Journal of Mammalogy 74: 715-722).

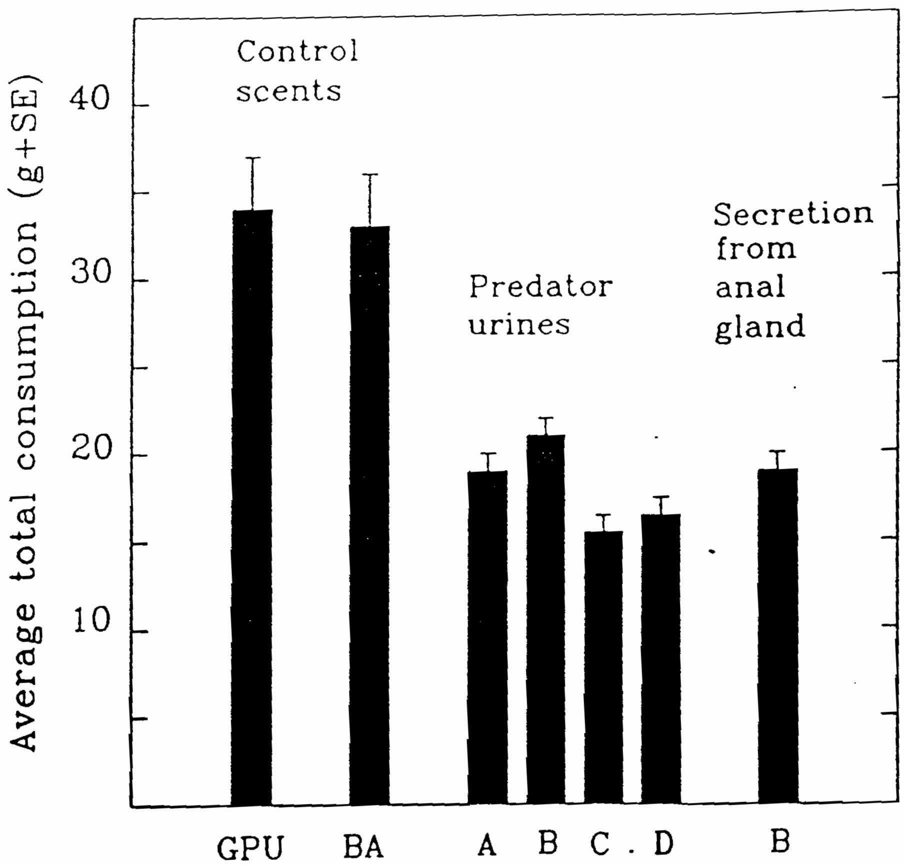
Figure 3. Mean change in total distance travelled (cm) by sham operated (control) and anosmic fathead minnows following exposure to chemical stimuli from northern pike. (From: Chivers, D. P., and R. J. F. Smith. 1993. The role of olfaction in chemosensory-based predator recognition in the fathead minnow, *Pimephales promelas*. Journal of Chemical Ecology. 19: 623-633.

Figure 1.



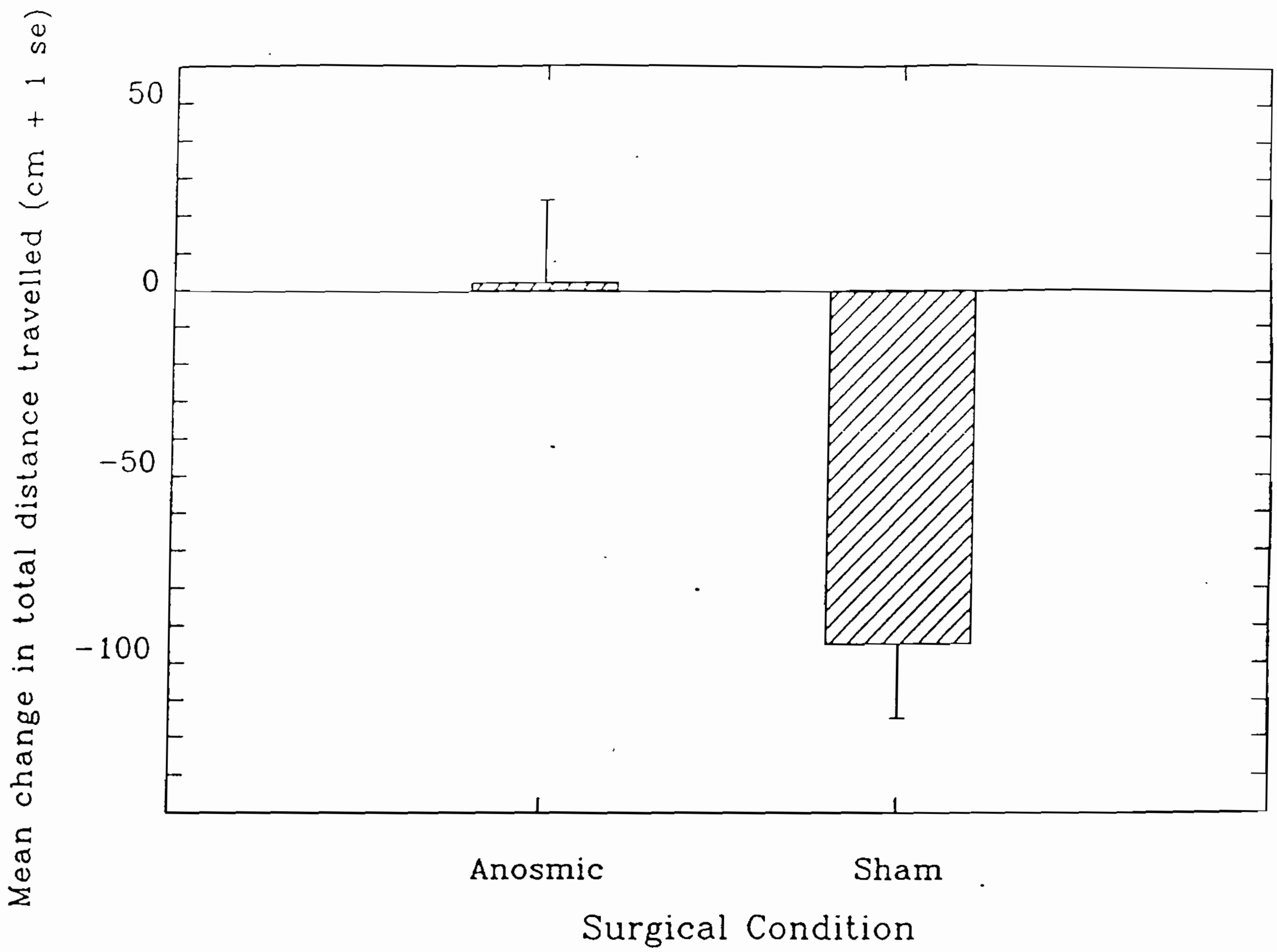
EPA
EPA + CS2
% CS2
BAIT CONSUMED (grams)
80
60
40
20
1
2
3
4
5
6
TEST REPLICATES
80
60
40
20
% CS2 OF TOTAL

Figure 2.



Control
scents
Predator
urines
Secretion
from
anal
gland
Average total consumption (g+SE)
40
30
20
10
GPU
BA
A
B
C
D
B

Figure 3.



Mean change in total distance travelled (cm + 1 se)
50
0
-50
-100
Anosmic
Sham
Surgical Condition